

SHORT COMMUNICATION

MALE EGG GUARDING BEHAVIOR IN THE NEOTROPICAL HARVESTMAN *AMPHERES LEUCOPHEUS* (MELLO-LEITÃO 1922) (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. Males of the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão 1922) were observed guarding egg-batches attached to the undersurface of leaves. As recorded for other paternal harvestmen, males of *A. leucopheus* guard egg-batches containing eggs in different developmental stages as well as newly hatched nymphs. This is the second case of paternal care recorded among gonyleptids and the fifth in the order Opiliones.

Keywords: Harvestmen, Caelopyginae, parental care, postzygotic investment

Egg guarding behavior is present in all orders of Arachnida, but exclusive postzygotic paternal investment is restricted to members of the order Opiliones. Four cases have been recorded so far. Males of *Zygopachylus albomarginis* (Chamberlin 1925), a Manaosbiidae from Panama, build a cup-like nest on tree trunks made of mud and debris. During the breeding season the mud nests may be inspected by several females that occasionally lay 1-5 eggs. After oviposition, females leave the nests and the males remove fungi, chase potential predators away and prevent cannibalism (Rodriguez & Guerrero 1976; Mora 1990). In *Lepchana spinipalpis* Roewer 1927, an Assamiidae from Nepal and *Gonyleptes saprophilus* Mello-Leitão 1922, a Gonyleptidae from southeastern Brazil, males guard an egg-batch containing eggs in different developmental stages and even newly hatched nymphs (Martens 1993; Machado & Raimundo 2001). In these cases, possibly more than one female contributes to the batch at different times, as recorded for *Z. albomarginis*. In *Leytodoxis oviger* Martens 1993, a Podoctidae from the Philippines, females attach four or five eggs directly to the fourth femur of the males that carry the eggs until they hatch (Martens 1993).

Incipient cases of biparental care or an "alternative" form of paternal care were observed among goniosomatines, in which males are able to care for the brood when guarding females desert or die. Males of *Goniosoma longipes* (Roewer 1913)

(Gonyleptidae, Goniosomatinae) may defend a territory on a cave wall where females lay eggs and take care of their batches (Machado & Oliveira 1998). If a female is experimentally removed from her egg-batch, the male guards eggs for up to two weeks (Machado & Oliveira 1998). Similarly, in *G. albipunctum* Mello-Leitão 1932, whose females also regularly take care of the offspring, a male was once observed guarding eggs and nymphs in the field (Willemart & Gnaspini in press). Additionally, in *G. spelaeum* (Mello-Leitão 1923) several males were observed close to guarding females (Gnaspini 1995), suggesting that males could either defend his mate and/or occasionally defend the offspring. Machado & Raimundo (2001) suggest that the association between males and their offspring through the defense of an oviposition site may constitute the basis for the evolution of paternal care in most harvestmen species.

In this paper we report a new case of male egg guarding behavior in harvestmen. *Ampheres leucopheus* (Mello-Leitão 1922) belongs to the subfamily Caelopyginae (Gonyleptidae) and inhabits the rain forests of southern and southeastern Brazil. Behavioral observations were conducted in the laboratory on a guarding male captured at Parque Estadual Intervales (Ribeirão Grande, São Paulo State) in February 2000. The branch containing the egg-batch and the guarding male was taken to the laboratory to investigate if the parental individual

would also care for nymphs. The male and the egg-batch were maintained in a plastic box ($17 \times 13 \times 10$ cm) for three days until the hatching of the first nymphs, at around 25°C and relative humidity of 70–80%. Twenty-four hours after the hatching of the first nymphs, the male, juveniles and remaining eggs were preserved in 70% ethanol. Measurements of egg diameter were taken with calipers (0.01 mm) before preservation. To assess the fecundity of females, ten preserved individuals collected in localities near the study sites were dissected and the number of eggs in the reproductive tract was counted. The dissected individuals were deposited at Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo State, Brazil (numbers: HS 256, 6541, 14133, and 14199).

Field observations were conducted on three guarding males found near Guaricana Dam (São José dos Pinhais, Paraná State) in December 2001. The presence of these three guarding males near the eggs were checked four times during one afternoon (1300–1900 h), totaling 12 events of field observation. Each observation event lasted 5–10 min. Voucher specimens were deposited at Museu de Zoologia da Universidade de São Paulo and Museu de História Natural da Universidade Estadual de Campinas (ZUEC), São Paulo State, Brazil.

Egg-batches were laid on the underside surface of leaves, attached by a very abundant transparent mucous layer (Fig. 1). The three egg-batches observed directly in the field contained more than 100 eggs (165 eggs in Fig. 1; eggs of the other two were not counted), and the one taken to the laboratory contained 216 eggs. Like many laniatorean harvestmen (Gnaspini 1995; Machado & Oliveira 1998), eggs of *A. leucopheus* darken during the embryonic development: recently laid eggs are white or yellowish, and just prior to hatching they are dark brown with many black spots. A curious pattern observed in all four egg-batches (see Fig. 1) is that older eggs were placed closer to the leaf apex, probably meaning that eggs are laid from the leaf apex towards its base, where the male rests. The average diameter of the eggs taken to the laboratory, measured just before hatching, was 1.42 mm ($\text{SD} = 0.10$ mm; range = 1.24–1.52; $n = 10$). From this egg-batch, 140 nymphs hatched within two days and the remaining 76 eggs were in an intermediate stage of development (based on the external coloration). Had the male been cannibalizing the eggs, we would expect a reduction in the number of eggs over time. Reduction in the number of eggs was observed neither in the field nor in the laboratory. In addition, the males were observed in a typical resting posture that was very similar to the posture of guarding females (see below), and not in their activity posture that would be needed if they were eating the eggs.

Of the ten dissected females, six contained eggs

in the reproductive tract. The number of mature eggs ranged from 20–36 (mean \pm SD = 28.2 ± 5.7), much less than the total number of eggs found in each batch in the field. This pattern differs from several species presenting only maternal care, such as *Goniosoma longipes*, *Goniosoma* aff. *proximum*, *Neosadocus* sp. and *Discocyrtus oliverioi* H. Soares 1945, in which the number of eggs in the female reproductive tract is similar to that observed in batches found in the field (G. Machado unpub. data). This suggests that males accept eggs from more than one female or from the same female at different times. Although the second hypothesis seems to be unlikely, some guarding females of *Goniosoma* are known to copulate when guarding their eggs, and to add a few eggs to the batch during the brooding period (Gnaspini 1995; Machado & Oliveira 1998).

In eight out of the 12 field observations, males of *A. leucopheus* were seen resting near the eggs (Fig. 1), with no specific behavior toward the eggs, similar to the posture and behavior adopted by guarding females of several other harvestmen (see Gnaspini 1995; Machado & Oliveira 1998). In the remaining four events, however, the guarding males were not observed near the egg-batches. While one male was always seen close to the eggs, a second male was not seen near the eggs twice and a third male was not seen close to the eggs also twice. In one of these cases, the male was back to his guarding position in the following sampling event. In another case, the male was seen walking near the stem of the tree (ca. 20 cm from the leaf with his egg-batch) towards the canopy. It is possible that the males were guarding their batches at distance or even patrolling the surrounding area, as occurs in *Z. albomarginis* (Mora 1990). This behavior contrasts with that of egg-guarding females, which do not leave their egg-batches, even to forage (e.g., Gnaspini 1995; Machado & Oliveira 1998). However, in the laboratory, the male remained near the offspring even after the hatching of the first nymphs.

Although we have only a few observations and little is known about the reproductive biology of Caelopyginae, we suggest that the behavior observed in *A. leucopheus* is a case of exclusive paternal care. We suggest that the hypothesis of “alternative” paternal care, like that observed for some Goniosomatinae species (Machado & Oliveira 1998; Willemart & Gnaspini in press), is unlikely for *A. leucopheus*. If it was the case, we would expect to find some egg-batches guarded by females, but we observed none, even though the species was reproductively active.

Recently, Tallamy (2001) analyzed all described cases of exclusive paternal care in arthropods and suggested that male guarding behavior could release females from the fecundity constraints of maternal



Figure 1.—Male of *Ampheres leucopheus* (body length = 1 cm) in resting position near eggs laid on the underside surface of a leaf in the forest near Guaricana Dam, São José dos Pinhais, Paraná State, Brazil.

care and provide an honest signal of paternal intent and quality. Therefore, males that are willing to take care of the offspring become preferred mates for females and may achieve a greater number of copulations than males that are unwilling or unable to care for eggs. The predictions of exclusive paternal care as a sexually-selected male trait are: (a) females are iteroparous; (b) there are many mating opportunities for the males; (c) care interferes with female foraging; (d) eggs increase male attractiveness; (e) males may guard eggs laid by several females; (f) males are willing to guard unrelated eggs and (g) the local female population is high (Tallamy 2001). At least *Z. albomarginis*, *L. spinipalpes* and *G. saprophilus* fit well to most of these predictions. For *A. leucopheus*, however, detailed observations in the field are needed to allow proper conclusions, but these preliminary results seem to corroborate a crucial point of Tallamy's hypothesis: males may

guard eggs from more than one female, as discussed before.

This is the second case of exclusive paternal care described for members of the large family Gonyleptidae (see Machado & Raimundo 2001). Because *G. saprophilus* belongs to the subfamily Gonyleptinae, which is not closely related to Caelopyginae (see Pinto-da-Rocha 2002), it is possible that paternal care in gonyleptid harvestmen evolved independently. In addition, "alternative" paternal care evolved in a third and unrelated subfamily, the Goniosomatinae. In the future, behavioral studies on other species of Gonyleptidae allied with the phylogenetic information (Pinto-da-Rocha 2002) could help to answer how many times paternal care has evolved within the family and if male guarding in harvestmen evolved from no care or from female care. Finally, it is possible that paternal care among harvestmen is more common than previously

thought, and that more cases will be detected when a larger number of species are studied, especially the tropical laniatoreans.

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